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AN ARRANGEMENT OF THE RETINAL CELLS IN THE EYES OF FISHES PARTIALLY SIMULATING COMPOUND EYES.

BY JOHN A. RYDER.

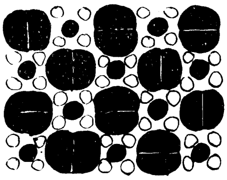
The peculiar structure of the compound eyes of the Arthropods has attracted a large share of attention from such investigators as Grenacher, Lankester, Watasé, Patten, Carrière and others. The peculiarities of structure of compound eyes are so marked that it would be strange if they failed to attract the notice of students of morphology. In the vertebrates the structure of the retina is universally regarded as differing so widely from that of the compound type of eye found in the Arthropods, that few authors have been tempted to institute any very close morphological comparison between them. I should not attempt such a comparison were it not that I have recently found that in the eye of the larval salmon, *Salmo salar*, there is an arrangement of the sensory cells of the retinal epithelium that is so regularly and definitely repeated throughout the whole extent of the retina as to admit of no question.

The observations upon which my statements rest were made upon certain very thin sections of recently hatched salmon larvæ. These sections were prepared for an entirely different purpose, and it was only upon casual observation that the peculiarities I am about to describe were first noticed.

These sections ranged from 2.5 to 5 mikrons in thickness, and no doubt can be thrown upon my observations on the score of faulty technique. The specimens had been splendidly fixed and preserved and were stained *in toto* in an alcoholic solution of hæmatoxylin, and differentiated *in toto* in a one per cent. solution of potassium bichromate. This method leaves but little to be desired for clearness of histological differentiation and sharpness of detail. Unfortunately, it is only a very few sections out of a complete series that reveal the details that are to be described. These few sections are the first three or four that were cut tangentially to the surface of the retina, and that which is cut just through the ends of the rods and cones and cone-cells, at about the level of the inner or under side of the layer of retinal pigment. One, therefore, only obtains six to eight sections in sectioning an entire eye; that is, three or four just as the surface of the retina is reached by the knife, and again just as it leaves off cutting through the retina at the opposite side of the eyeball. In other words, very superficial tangential sections only, or such as are cut in a plane very nearly coincident with the bacillary or Jacob's layer will show the regular repetition of structure that impels me to make a comparison between the compound eyes of Arthropods and the retinal structure of the larval salmon.

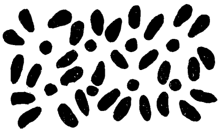
The first thing that strikes the observer in examining such sections is the extraordinary regularity with which the bacillary portions of the retinal elements are arranged. One notices that the rods and cones form together a pattern of the most astonishing regularity. That the rods are in groups of four or five, but that the cones are much larger across and always in pairs, or of the nature of Hannover's double cones and united together closely at their apices. These double cones are arranged in rows in two ways at right angles to each other, like the squares on a chess-board, Fig. 1. If one now imagines the rows of double cones to represent the black squares of a chess-board, the groups of rods, which are much smaller in cross-section, may be regarded as occupying the intervening red squares. This is the appearance of a section taken at the outermost level. Pigment from the pigmented layer extends in between the rods and cones, and the distinctness of the regular retinal pattern is thus greatly heightened. In the next section, only 2.5 to 5 mikrons below the level at which the extreme regularity of pattern just described appears, there is another pattern formed by the rods and cones, which shows that the bodies of the pairs have slightly separated from one another. The continuations of the double cones of Hannover are now also seen to be less

FIG. 1.



densely stained, and while still showing a paired condition are no longer in contact, and no longer have their adjacent faces flattened as when united, as in the preceding section. One may now count eight cone cells arranged in four groups, of two each, around a single very distinct rod, Fig. 2. This arrangement is at first somewhat difficult to make out, but it requires only a short time for the observer to convince himself that a regular arrangement of the rods and cones also obtains at this lower level. This evidence conclusively establishes the fact that every one to five rod-cells in the eye of a larval salmon are surrounded by eight cone-cells that are closely opposed or united at their apices into four pairs of two each. At a slightly deeper level the bodies of the pairs of cones separate still more, but traces of a regular pattern can still be made out at a third level.

FIG. 2.



I have stated in the title of this paper that there is an arrangement of retinal cells of fishes that partially simulates that of the retinal elements in the compound eyes of Arthropods. This definite proviso is necessary because the comparison between the groups consisting of four or five rod-cells and four double cones in the retina of the salmon cannot be exactly homologized with the cell-groups known as ommatidia in the Arthropod eye. In the latter each ommatidium is distinct from its adjacent fellows and none of its cellular elements enter into the formation of the contiguous ommatidia by which it is encircled. In the retina of the larval salmon the case is very different and quite peculiar. Of any one group consisting of five central rod-cells and four double cone-cells, the latter also enter into the formation and form part of eight adjacent similar groups of cells. Into four of the eight adjacent groups two double cone-cells enter, and, alternating with these are four other groups into which only a single pair of the double cone-cells of the central group enters. The comparison is therefore only a partial one. It is obviously absurd to suggest the complete homology of a group consisting of the five central rod-cells and their four surrounding double cones in the retina of the salmon with a single ommatidium of the Arthropod eye.

To what extent a similar condition holds in the arrangement of the bacillary retinal elements in other groups of vertebrates I am not prepared to say. But this remarkable regularity and repetition of arrangement of cellular elements in the retina of a fish is at least very suggestive. Blaue has shown that the olfactory organ of fishes is made up in some cases of very small discrete sense-organs simulating the structure of taste-buds and the small circular sensory buds found in the lateral line organs of fishes. Ayers has traced the probable origin of the complex sensory structures found in the cochlea of vertebrates to a multiplication and subsequent coalescence of originally discrete sense-buds or end-organs, that arose in a way similar to the discrete end-organs of the lateral line. The detection of regularly repeated groups of sense-cells in the retina of one of the lower vertebrates thus becomes highly significant. Is it possible, after all, that the retina of vertebrates has been evolved by the coalescence of very small groups of sense-cells that were at one time separate and simple sense-organs, just as the complex olfactory and auditory sensory epithelia of vertebrates appear to have so arisen? The arrangement that has been described appears to extend throughout the whole of the functional part of the retina of the larval salmon, so that the grouping of the cells is at least uniform in this type during the early stage of its existence. This is a feature that is in strong contrast with that met with in the retinæ of mammals, in which the distribution of rods and cones is not uniform over the whole functional surface of the organ. If, however, there is any truth in the suggestion that the retina of the higher vertebrates has arisen in the same way as the sensory epithelia of the olfactory and auditory organs, namely by the coalescence of originally distinct but repeated, similar sense-organs, then the arrangement that we actually find in the retina of the salmon approximates such a primitive condition of structure, though by no means as perfectly as is seen in the compound eyes of Arthropods.

It may be added that the reason that I assume such a regularly repeated structure recurs throughout the whole of the retina of the young salmon, is because it is found that whenever the planes of meridional sections coincide with rows of double cones, the latter alternate, in vertical sections of the retina also, and with the utmost regularity with the single central rod elements. Such alternating rods and double cones are met with only in sectious cut through the greatest diameter of the eye and exactly vertical to the maximum thickness of the retina, as should be expected from the manner of arrangement of the rods and cones, as seen in sections that are cut horizontally through the bacillary layer and parallel to a plane tangent to its convex surface.

Max Schultze has figured portions of the bacillary layer of the retina of mammals, as seen from the surface, and one sees in such figures that the cones are repeated at regular intervals, the more numerous rods surrounding the cones. In the retina of the salmon this arrangement is reversed, or at least is not so obvious unless one assumes that every double cone in this form is supposed to be encircled by eight rods. In the salmon the cone elements are most numerous; in mammals they are less numerous than the rods over a very large portion of the retinal surface. These facts together with the rest of what has preceded do not conflict, however, with the view that the groups of cells met with in the retina of the young salmon are fairly to be regarded as having arisen from a condition in which such groups of rods and cones were more or less distinct and separate as in the compound eyes of Arthropods. On morphological grounds alone, it seems to me, that we are driven to some such conclusion. No matter what convictions one may hold as to the utter untenability of any hypothesis that seeks to derive the vertebrates from the Arthropods or *vice versa,* it seems probable from the evidence now at hand, that highly complex and specialized sense-organs of all kinds, including, possibly, the retina of vertebrates, have arisen by the coalescence of simpler, smaller and more numerous sensory organs. That the sense-organs of both vertebrates and Arthropods have pursued parallel paths in the course of their evolution seems highly probable. The frequency with which specialization, reduction and even apparent simplification, in some respects, of organs, in the course of organic evolution, is associated with a process of coalescence of more numerous structures having the same function, is very strongly in favor of such a conclusion.

The single groups of retinal elements in the retina of *Salmo,* comprising, as we have seen above, thirteen cells, I propose to call *retinidia* in contradistinction to what is met with in the Arthropod eye, where the single visual organs are known as ommatidia. This distinction is a necessary one in view of the fact that it is obviously impossible to assert, in the face of the morphological evidence, that there is an exact homology between what are known as ommatidia and the cell-groups in *Salmo* that I have called retinidia. I have found it difficult to determine the exact number of rod-cells in the center of the groups. As nearly as can be made out with an immersion $\frac{1}{12}$ there are five. At first when this regularity of structure of the salmon's retina was noticed with low powers it was supposed that there was only one rod-cell in the centre of each retinidial group. The overlapping or blending of these groups with one another in *Salmo* is shown in both Figs. 1 and 2, and this is the one feature that makes it impossible to homologize them exactly with the ommatidia of the compound eyes of Arthropods.